GENETICS

Genetic analysis for dynamic changes of egg weight in 2 chicken lines

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ABSTRACT One of the main concerns for poultry producers is how to maintain egg uniformity and stability in size and weight following the rapid growth during the early laying period. In this study, we aimed to investigate the increase in egg weight with advancing hen age, and to estimate genetic parameters of these increment traits in 2 pure lines of chickens (i.e., 2,010 White Leghorns and 1,200 brown-egg dwarf hens), using the restricted maximum likelihood method with the DMU procedure. We collected age at first egg (AFE), first egg weight (FEW) and kept records of egg weight per 10 wk from 30 to 60 wk of age. Meanwhile, the increments of egg weight were calculated for the evaluation of age-dependent dynamic changes. The increment of egg weight gained dramatically before 30 wk of age and became slower with the advance of age. Heritability estimates of AFE were larger than 0.32, and the low to moderate genetic correlations between AFE and FEW were observed in the 2 lines. The FEW showed high variation level compared with egg weights at later ages in the 2 lines, and had moderate heritability estimates in White Leghorns (0.20) and dwarf hens (0.33). Egg weights at different ages were highly heritable in the 2 lines (h² ≥ 0.35), and had strong genetic and phenotypic correlations among different ages. The estimates of heritability for most increment traits were low to moderate, especially those increments for 10-wk intervals ranging from 0.00 to 0.14. The genetic correlations among 3 consecutive egg weight increments for 10-wk intervals were low to moderate. Our results in the 2 lines should provide important insights into the genetic architecture of increment traits and offer some suggestions for producing uniform and stable eggs in response to advancing age.

Key words: egg weight, increment trait, dynamic change, genetic parameter, restricted maximum likelihood

INTRODUCTION

Egg weight has great economic importance in poultry breeding and is considered as among the major breeding objectives and research goals in different countries (Shalev and Pasternak, 1993; Jones et al., 2001; Johnston and Gous, 2007; Islam and Dutta, 2010; Savegnago et al., 2011). Nowadays, with the rapid development of mechanical automation, eggs with uniform size and weight are especially desired for automatic packing (Wolc et al., 2012). Due to different size preferences, egg consumption is highly diverse around the world [e.g., many consumers prefer relatively large eggs in some Western countries, as opposed to China (Jones et al., 2001; Koelkebeck et al., 2001)]. Moreover, egg weight has been reported to have a crucial effect on chick quality including hatchability, hatch weight, fitness, and chick performance (Pinchasov, 1991; Hartmann et al., 2003; Enting et al., 2007; Nangsuay et al., 2011). Therefore, producing eggs of appropriate size and weight is a key issue for both producers and breeders.

From an economic point of view, it is desired that eggs quickly reach appropriate weight around laying peak, and then maintain good uniformity and stability without significant increase in the following laying period (Poggenpoel and Duckitt, 1988; Shalev and Pasternak, 1993). Numerous previous studies suggested that egg weight showed a curvilinear relationship with the increase of hen age (Di Masso et al., 1998; Suk and Park, 2001; Nangsuay et al., 2011; Tumova and Gous, 2012), and provided critical insights into controlling the increase rate of egg weight (Minvielle et al., 1994). However, these authors only evaluated the tendency and increment of egg weight between different weeks of age, lacking full evaluation of their genetic basis. So far, only sporadic relevant work on evaluation of genetic parameters for the increment of egg weight in chickens was reported over the past decades (Clayton and Robertson, 1966; Poggenpoel and Duckitt, 1988; Shalev and Pasternak, 1993). Comprehensive estimation of genetic parameters for these traits is essential.

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to investigate the age-dependent dynamic changes and factors influencing egg weight increments.

In this study, we regarded the increment of egg weight as a novel and significant target trait (increment trait) and performed genetic analysis in 2 pure lines to elucidate the variation levels in egg weight with advancing hen age. The comprehensive exploration of dynamic changes of egg weight is essential for future research controlling egg size and weight variation throughout the whole laying period of chickens.

**MATERIALS AND METHODS**

**Experimental Population**

Two pure lines of White Leghorns (WL) and brown-egg dwarf hens (DW), maintained and selected mainly for egg production for more than 10 yr in the Poultry Genetic Resource and Breeding Experimental Unit of China Agricultural University (Zhang et al., 2005), were used in this study. These 2 populations were produced from pedigree mating using 50 sires and 7 to 8 dams per sire for each line. Eggs obtained from these families with full pedigree were hatched at the same time. Chicks were vent sexed, wing-banded, and vaccinated against Marek’s disease at hatch. Chicks were raised according to conventional management. At 16 wk of age, 2,010 WL and 1,200 DW pullets were transferred to 3-tier single-hen cages in a randomized design in the open-sided laying house. The photoperiod was increased by 1 h per week from natural light until 16 h of light per day was achieved.

**Traits Measured**

At about 20 wk of age when hens started laying, the age of first egg (AFE) and first egg weight (FEW) of all hens were recorded. Subsequently, egg weights were measured on 3 consecutive days per 10 wk from 30 to 60 wk of age in the 2 lines, and the average for 3 d was regarded as the phenotypic value for each hen. Cracked, soft-shell, and double-yolked eggs were not used in our study. The egg weights were labeled as EW30, EW40, EW50, and EW60 from 30 to 60 wk. Meanwhile, to assess the dynamic changes in egg weight, the egg weight increments between different week of age were calculated, respectively. For instance, the egg weight increment from AFE to 30 wk of age was defined as the difference between 2 egg weight values and was referred to as IEW03, and other traits can be deduced by analogy, such as IEW34 = EW40 − EW30. In addition, we used the CV of egg weight at a specific age to evaluate egg uniformity in the population, which could more properly compare the results from different ages.

**Statistical Analysis**

Descriptive statistics were calculated with the MEANS procedure of the SAS software package (SAS Institute Inc., Cary, NC) using all available records. In the present study, the 2 lines of experimental chickens came from one generation with the same sex and were raised in the same house under the same environment, so there were no other known fixed nongenetic effects affecting the results. Though we have detailed pedigree information over 10 generations, only 4 generations were adopted to estimate genetic parameters due to the limited genetic information from more distant relationships. Genetic parameter estimates for egg weight and corresponding increment traits were obtained for each line separately, based on an animal model as follows:

\[ Y_{ij} = \mu + a_i + e_{ij}, \]

where \( Y_{ij} \) = the \( ij \)th observation of egg weights and corresponding increment traits, \( \mu \) = the population mean, \( a_i \) = random additive genetic effects of hen \( i \), and \( e_{ij} \) = random residual error.

For this purpose, covariance components, genetic parameters, and corresponding SE were estimated using the restricted maximum likelihood implemented in the DMU software package with an average information algorithm for analysis of multivariate mixed models (Klein et al., 1973; Hamrup et al., 2000; Madsen and Jensen, 2008).

**RESULTS**

**Descriptive Statistics of Egg Weight Traits**

The detailed description of means, SD, and CV of AFE, egg weights measured in the different weeks of age and corresponding increments are shown in Table 1. The WL showed more early and uniform AFE than DW. The averages of FEW in WL and DW were 34.32 ± 4.38 and 33.29 ± 5.09 g, respectively. As shown in Figure 1A, egg weights increased curvilinearly with advancing age in the 2 lines. Moreover, almost all egg weights in WL were greater than the corresponding traits in DW at the same age.

In the 2 lines, these egg weight increments demonstrated similar age-dependent dynamic change patterns (Figure 1A and 1B). The average increment for egg weight from AFE to 30 wk of age was larger than other age intervals in the entire laying period. Almost all increments of egg weight decreased with increased age, whereas egg weight no longer increased after 50 wk. In terms of egg uniformity, FEW demonstrated high variability in the 2 lines.

**Estimation of Genetic Parameters**

Considering that AFE may have a crucial effect on FEW, we evaluated the potential relationship between them. The AFE showed high heritability estimates in the 2 lines. Estimates of heritability for FEW in the 2 lines were 0.20 and 0.33, respectively. It should be noted that both genetic and phenotypic correlation estimates...
between AFE and FEW (0.04 and 0.17) in WL were smaller than in DW (0.52 and 0.44). From 30 wk of age on, all egg weights were highly heritable in the 2 lines, ranging from 0.35 to 0.60 (Table 2). All egg weights from 30 to 60 wk of age showed strong and positive genetic and phenotypic correlation between these traits and had similar genetic architectures in the 2 lines.

We divided the whole laying period into 2 parts based on 30 wk of age being around the laying peak. Considering the largest magnitude of IEW03 throughout the laying period, we first analyzed the genetic relationship between IEW03 and egg weights at AFE and 60 wk of age to evaluate the potential factors implicated in early increments and late egg weight. The genetic parameters for FEW, IEW03, and EW60 are summarized in Table 3. The IEW03 in WL showed a low heritability (0.11). The FEW showed low negative genetic correlations, but strong negative phenotypic correlation with IEW03 in the 2 lines.

We also estimated the genetic correlations between egg weight at 30 wk of age and corresponding increment traits. Our results suggested that these traits had low to moderate genetic correlations (Tables 4 and 5). Among all increment traits, most heritability estimates were very low, except that IEW36 (0.35) showed high heritability estimates in the dwarf hens. Meanwhile, genetic and phenotypic correlations among 3 consecutive increment traits for 10-wk intervals were low to moderate in the 2 lines. Most increment traits for 10-wk intervals presented lower heritability estimates than corresponding increment traits for 20- to 30-wk intervals. It should be noted that the SE of genetic correlations

![Figure 1. Dynamic changes of egg weight with advancing hen age in the 2 lines. A) Age-dependent changes of egg weight in the 2 lines. B) Increments of egg weight for 4 intervals in the 2 lines. WL: White Leghorn; DW: dwarf layers. AFE = age at first egg; IEW = egg weight increment from early to late age.](https://academic.oup.com/ps/article-abstract/93/12/2963/2730290)

Table 1. Descriptive statistics for age at first egg (AFE), egg weights (EW), and corresponding increments in White Leghorns (WL) and dwarf layers (DW)

<table>
<thead>
<tr>
<th>Trait (g)</th>
<th>Age/interval (wk)</th>
<th>WL</th>
<th>DW</th>
</tr>
</thead>
<tbody>
<tr>
<td>AFE</td>
<td>—</td>
<td>133.85 ± 5.65</td>
<td>134.88 ± 9.47</td>
</tr>
<tr>
<td>EW</td>
<td>AFE</td>
<td>34.32 ± 4.38</td>
<td>33.29 ± 5.09</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>49.53 ± 3.49</td>
<td>47.01 ± 3.51</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>53.41 ± 3.89</td>
<td>51.71 ± 4.14</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>57.14 ± 4.10</td>
<td>55.30 ± 4.70</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>57.50 ± 4.28</td>
<td>56.64 ± 5.10</td>
</tr>
<tr>
<td>IEW</td>
<td>03</td>
<td>15.23 ± 4.51</td>
<td>13.66 ± 5.00</td>
</tr>
<tr>
<td></td>
<td>34</td>
<td>3.83 ± 2.54</td>
<td>4.65 ± 3.45</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>3.70 ± 2.65</td>
<td>3.59 ± 4.27</td>
</tr>
<tr>
<td></td>
<td>56</td>
<td>0.39 ± 2.68</td>
<td>1.26 ± 3.57</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>7.52 ± 2.79</td>
<td>8.17 ± 3.43</td>
</tr>
<tr>
<td></td>
<td>46</td>
<td>4.14 ± 3.18</td>
<td>4.85 ± 4.48</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>7.90 ± 3.23</td>
<td>9.43 ± 3.93</td>
</tr>
</tbody>
</table>

1IEW = increment of egg weight.

2EW30, EW40, EW50, EW60 = egg weight per 10 wk from 30 to 60 wk of age, respectively; intervals = age difference from early to late age (i.e., 03 = 30 wk – AFE).
between increments from 50 to 60 wk of age and the rest of the traits were quite high, reflecting the low heritability of corresponding traits.

**DISCUSSION**

Egg weights have always been an important issue for producers and customers, and there is not a “one size fits all” weight due to diverse markets in different countries (Gowe and Fairfull, 1995; Ledur et al., 2002). Currently, a common goal is to improve egg uniformity and stability in size and weight as hen age advances, which will be beneficial to automatic packing and growth in consumption (Emsley, 1997; Hester, 2005; Schreiweis et al., 2006; Johnston and Gous, 2007; Wolc et al., 2011, 2012). As the most important commercial strain, WL had slightly lower and more consistent AFE. The diverse AFE of DW pullets might lead to higher differences in FEW due to the positive correlation between hen age and egg weight (Niknafs et al., 2012). In this study, our findings about age-dependent changes are similar to some previous reports, that is, these egg weights increase curvilinearly with advancing hen age (Poggenpoel and Duckitt, 1988; Van Den Brand et al., 2004; Mertens et al., 2008; Nangsuay et al., 2011). The CV of egg weights similarly increased, suggesting that egg uniformity became worse with increased age. Because laying rate would decline as hen age advances and vary greatly among different individuals, the antagonistic relationship between egg number and egg weight demonstrated that chickens with lower rate deposited more egg component weight in a longer laying time (Niknafs et al., 2012), resulting in higher variability of egg weight at later stages. The increase in egg weight gradually decreased with age and, even more so, I EW56 values were near zero, indicating that egg weights remain relatively stable in the late laying period (Mertens et al., 2008; Islam and Dutta, 2010).

To understand the genetic basic and key factors dominating dynamic changes in egg weight, we estimated genetic parameters of egg weight and corresponding increment traits. In accordance with the previous studies (Lwelamira et al., 2009; Niknafs et al., 2012), AFE also showed high heritability in this study. The lower genetic and phenotypic correlation estimates between AFE and FEW in WL compared with DW may be due to lower genetic variation within the WL population. In spite of some difference in the 2 lines, the moderate genetic correlations between AFE and FEW suggested that the diverse AFE might contribute significantly to the dramatic changes of FEW. Heritability estimates for FEW were moderate to high, similar to a lot of other studies (Lwelamira et al., 2009; Wolc et al., 2011), but somewhat higher (Hagger, 1994; Savegnago et al., 2011) or lower (Sang et al., 2006; Dana et al., 2011) estimates have also been reported. The estimated heritabilities of egg weights at different ages coincided with the estimates from many relevant studies (Zhang et al., 2005; Begli et al., 2010), but were slightly higher than
other studies (Buitenhuis et al., 2004; Savegnago et al., 2011). Moreover, genetic correlations between early and late egg weights were relatively high in agreement with the previous studies (Sang et al., 2006; Niknafs et al., 2012), showing that early egg weight has a significant effect on later egg weight and can act as an indicator of subsequent egg weight. These high heritability estimates of egg weights indicated the existence of substantial additive genetic variation, which is the genetic basis of individual selection and early selection (Niknafs et al., 2012). Similarly, to improve egg uniformity, breeders can select those individuals with uniform egg weight and size at the same age in a breeding program.

Few studies of genetic parameters for increment traits have been reported and our study revealed findings that may be of interest. Heritability estimates of IEW03 in WL and DW are mostly low. Most increment traits for 10-wk intervals also showed low heritabilities. Relatively, the magnitude of heritability estimates of most increment traits for 20- and 30-wk intervals were moderate. This increasing trend may indicate that additive genetic variance increased with age for egg weight (Ledur et al., 2003; Niknafs et al., 2012). Two previous studies reported that egg weight increments from 210 to 310 d were much more affected by environmental factors (Poggenpoel and Duckitt, 1988; Shalev and Pasternak, 1993), implying a larger contribution of environmental variance, similar to our results. Overall, the low and moderate heritability estimates of increment traits indicate that it is a big challenge to achieve our expected goals by traditional breeding methods. Some approaches such as marker-assisted selection may be a good alternative for selection of these traits, especially early increment traits (Kapell et al., 2012).

In our results, some increment traits showed low heritabilities, a little different and even opposite in sign between genetic and phenotypic correlation, showing significant influence of environmental factors between 2 increment traits. Genetic correlations between traits in 30 wk and most corresponding increment traits were low to moderate, suggesting that using the traits in specified age to predict their subsequent increments should be careful because the accuracy may be relatively low (Shalev and Pasternak, 1993). It should be noted that the low genetic correlations among 3 consecutive egg weight increments for 10-wk interval may indicate independent increasing patterns along with hen ages. Meanwhile, the genetic correlations between IEW56 and other corresponding traits in the 2 lines were estimated with large SE. The SE is function of the magnitude of the heritabilities and the genetic correlations and can be estimated by an approximate formula given by the previous reports (Klein et al., 1973; Hannrup et al., 2000), suggesting that significantly small heritability estimates of these traits resulted in less precise estimates.

In conclusion, we investigated the dynamic changes of egg weight and estimated the genetic parameters of corresponding increment traits. Our results show that these low heritable increment traits are less determined by genetic factors. To achieve proper weight and egg uniformity and stability, we should focus on selecting those hens with appreciate egg weight around laying peak, and control the dynamic changes via novel marker-assisted selection and environmental regulation.

### Table 4. Heritabilities and genetic and phenotypic correlations for EW increment traits in White Leghorn

<table>
<thead>
<tr>
<th>Trait2</th>
<th>EW30</th>
<th>IEW34</th>
<th>IEW45</th>
<th>IEW56</th>
<th>IEW35</th>
<th>IEW46</th>
<th>IEW36</th>
</tr>
</thead>
<tbody>
<tr>
<td>AFE</td>
<td>0.46 (0.06)</td>
<td>0.19 (0.16)</td>
<td>0.65 (0.26)</td>
<td>-0.06 (0.36)</td>
<td>0.38 (0.22)</td>
<td>0.32 (0.15)</td>
<td></td>
</tr>
<tr>
<td>FEW</td>
<td>-0.18</td>
<td>0.09 (0.03)</td>
<td>0.57 (0.32)</td>
<td>0.71 (1.27)</td>
<td>0.43 (0.33)</td>
<td>0.87 (0.12)</td>
<td></td>
</tr>
<tr>
<td>IEW03</td>
<td>0.02</td>
<td>-0.44</td>
<td>0.05 (0.03)</td>
<td>0.81 (1.55)</td>
<td>0.99 (0.12)</td>
<td>0.89 (0.17)</td>
<td></td>
</tr>
<tr>
<td>EW60</td>
<td>-0.06</td>
<td>-0.05</td>
<td>-0.29</td>
<td>0.00 (0.02)</td>
<td>0.87 (1.01)</td>
<td>0.87 (0.12)</td>
<td></td>
</tr>
<tr>
<td>IEW21</td>
<td>-0.16</td>
<td>0.41</td>
<td>0.57</td>
<td>0.81 (0.06)</td>
<td>0.81 (0.18)</td>
<td>0.89 (0.17)</td>
<td></td>
</tr>
<tr>
<td>IEW36</td>
<td>-0.19</td>
<td>-0.41</td>
<td>0.61</td>
<td>0.21</td>
<td>0.05 (0.03)</td>
<td>0.78 (0.15)</td>
<td></td>
</tr>
<tr>
<td>IEW36</td>
<td>-0.05</td>
<td>0.41</td>
<td>0.26</td>
<td>0.58</td>
<td>0.62</td>
<td>0.17 (0.05)</td>
<td></td>
</tr>
</tbody>
</table>

1Heritabilities are given on diagonal, genetic correlations above diagonal, and phenotypic correlations below diagonal. Standard errors of estimates are in parentheses.

2EW30 = egg weight at 30 wk; IEW = egg weight increment from early to late age.
Table 5. Heritabilities and genetic and phenotypic correlations for EW increment in dwarf layers

<table>
<thead>
<tr>
<th>Trait</th>
<th>EW30</th>
<th>IEW34</th>
<th>IEW45</th>
<th>IEW56</th>
<th>IEW35</th>
<th>IEW46</th>
<th>IEW36</th>
</tr>
</thead>
<tbody>
<tr>
<td>EW30</td>
<td>0.56 (0.08)</td>
<td>-0.37 (0.43)</td>
<td>0.82 (0.34)</td>
<td>0.24 (0.29)</td>
<td>0.37 (0.17)</td>
<td>0.56 (0.14)</td>
<td>0.29 (0.15)</td>
</tr>
<tr>
<td>EW34</td>
<td>0.60</td>
<td>0.08 (0.05)</td>
<td>-0.38 (0.35)</td>
<td>0.09 (0.47)</td>
<td>0.39 (0.31)</td>
<td>-0.15 (0.30)</td>
<td>0.22 (0.27)</td>
</tr>
<tr>
<td>IEW45</td>
<td>-0.38</td>
<td>-0.63</td>
<td>0.14 (0.06)</td>
<td>0.65 (0.53)</td>
<td>0.63 (0.18)</td>
<td>0.96 (0.10)</td>
<td>0.77 (0.18)</td>
</tr>
<tr>
<td>IEW56</td>
<td>0.08</td>
<td>0.09</td>
<td>-0.36</td>
<td>0.09 (0.06)</td>
<td>0.47 (0.42)</td>
<td>0.88 (0.22)</td>
<td>0.98 (0.18)</td>
</tr>
<tr>
<td>IEW35</td>
<td>-0.08</td>
<td>0.23</td>
<td>0.62</td>
<td>-0.35</td>
<td>0.17 (0.06)</td>
<td>0.75 (0.17)</td>
<td>0.96 (0.10)</td>
</tr>
<tr>
<td>IEW46</td>
<td>-0.05</td>
<td>-0.54</td>
<td>0.66</td>
<td>0.48</td>
<td>0.52</td>
<td>0.28 (0.08)</td>
<td>0.85 (0.07)</td>
</tr>
<tr>
<td>IEW36</td>
<td>0.17</td>
<td>0.27</td>
<td>0.22</td>
<td>0.62</td>
<td>0.54</td>
<td>0.69</td>
<td>0.35 (0.09)</td>
</tr>
</tbody>
</table>

1Heritabilities are given on diagonal, genetic correlations above diagonal, and phenotypic correlations below diagonal. Standard errors of estimates are in parentheses.

2EW30 = egg weight at 30 wk; IEW = egg weight increment from early to late age.

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